

**BIOTIC AND ABIOTIC FACTORS AFFECTING ABUNDANCE OF THE
AMERICAN BURYING BEETLE, *Nicrophorus americanus***

By

JESSICA N. HOOPS

Bachelor of Science in Biology
Oklahoma State University
Stillwater, Oklahoma
2009

Bachelor of Science in Animal Science
Oklahoma State University
Stillwater, Oklahoma
2009

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the degree of
MASTER OF SCIENCE
July 2017

**BIOTIC AND ABIOTIC FACTORS AFFECTING ABUNDANCE OF THE
AMERICAN BURYING BEETLE, *Nicrophorus americanus***

Thesis Approved:

Dr. Scott T. McMurry (thesis advisor)

Dr. Barney Luttbeg

Dr. Karen McBee

ACKNOWLEDGMENTS

My love of the natural world was instilled in me and cultivated by my father, Gary. From a very young age he taught me to question, to investigate, to just sit back and watch. There were many times along this journey in which he had faith in me when I had none in myself. His mentorship and constant reassurance during my life have been more valuable to me than he will ever realize, and I would not have gotten this far were it not for him. My mom, Barbara deserves all the thanks in the world! Her assistance has come in so many forms, be it helping gather field supplies, dog-sitting during field season, or helping to set traps in the field. I am so grateful to have such a kind woman as my friend and biggest supporter. My brother, Cody has also contributed to this project more than he realizes. Thank you for being my best friend. Thank you for reminding me that the end result would be worth it, for coming out to the field, for always being the comedic relief (and mechanic!), and for never letting me give up.

My advisor, Dr. Scott McMurry deserves a whole load of never-ending gratitude! I like to think he saw a little of himself in me the first day I sat in his office, inquiring about a position in his lab. I can't find the words to express how thankful I am that he took a chance on me. Dr. McMurry, I'm sure I have tested the limits of your patience on numerous occasions and caused you plenty of stress; I am so grateful to have had the opportunity to develop as a biologist under your mentorship. Exposure to your seemingly endless supply of knowledge has been a gift that can never be trumped.

Dr. Barney Luttbeg and Dr. Karen McBee were both wonderful resources for this project. Dr. Luttbeg's mastery of R and willingness to guide me through the statistical analysis was instrumental in completion of this project. Dr. McBee is a wonderful mammalogist whose expertise was extraordinarily helpful. I couldn't have asked for a better committee. Thank you both for your guidance, support and above all, your patience.

Courtney Gray is irreplaceable as far as field technicians go. Courtney was absolutely dedicated to the project from day one, never balking at hard/smelly/hot work, never complaining. She is brilliant; her knowledge of the natural world never failed to impress me. I tend to do things the hard way; Courtney's ability to find a more direct path without compromising the end goal was immeasurably valuable to this project. She kept me sane, participated in every single wild idea I had, and was instrumental in accurate data collection for two field seasons. Thanks, Court, for being my partner in crime, my anchor, my roadkill collector, my co-pilot and my friend. I could never have done this without you!

Kyle Risser, Tom Ferrari, Ariel Petrilla and Natalie Stone - the knowledge I have gained from each of you since we initially embarked on this project is remarkable. Thank you. Sharing a field house with you guys was the best experience I have had to date. Each of you is treasured deeply. Thanks to Matt Bell and Kinzie Lee for their support during my first field season. Memories of laughing with you will last a lifetime!

Oklahoma State University has felt like home for many years. However, it was my acceptance into the department of Zoology that changed my world. I was welcomed and treated as a colleague immediately. Here, I felt like I was finally where I belonged. So many people in the department to acknowledge, but special thanks go out to Taylor Neighbors, Patrick Cusaac,

Dale Daniel, Bill Mausbach, Adam Simpson and Brent Fetting. Each of you has dealt with my tears and occasional self-doubt, my forgetfulness, or my inability to operate office machinery; but each of you has also inspired and shaped me into a solid biologist, and for that I am always grateful.

Many thanks go out to Bill Starry and Ryan Toby of the Natural Resources and Land Management department at the McAlester Army Ammunitions Plant. Their willingness to help me find suitable sites and unparalleled knowledge of the land are much appreciated. The lessons learned from these men can never be replaced. Thanks are due to Drs. Carrie Hall and Daniel Howard of Augusta College in Sioux Falls, SD for providing hundreds of beetles for my lab trials. Other people not to be forgotten: Dr. David Williams, Dr. Karen Hickman, and Anita Barstow of the U.S. Fish and Wildlife Service.

Last but certainly not least, my gratitude goes out to my fiancé, Matt Rice. You immediately took an interest in my research, and I believe this achievement means as much to you as it does to me. Thank you for recognizing the passion inside of me, and helping me to make my dream a reality, despite the sacrifices you have made. Your investment can never be repaid. You provided unwavering support, encouragement, love and faith -- all have driven me further than I ever thought possible. Thank you.

JESSICA N. HOOPS

JULY 2017

BIOTIC AND ABIOTIC FACTORS AFFECTING ABUNDANCE OF THE AMERICAN
BURYING BEETLE, *Nicrophorus americanus*

ZOOLOGY

The American burying beetle (ABB) *Nicrophorus americanus* Oliver (Coleoptera: Silphidae) is one of several species of carrion beetles and is listed as endangered in the United States. Previous research suggests that ABB population numbers have been reduced by 90% across its former range. These beetles require vertebrate carcasses for feeding and reproductive purposes. Although ABB will utilize any size carcass for feeding, conventional wisdom indicates that 80-100 gram carcasses are optimal for reproduction. Studies aimed at elucidating biotic and abiotic factors influencing the survival of ABB are spurious. I investigated several factors potentially affecting ABB populations, including small mammal abundance, competition from vertebrate scavengers for carrion resources, and several habitat characteristics. In addition, I attempted to determine if ABB exhibit preference regarding carcass body size for breeding. Results indicate a positive relationship between ABB and the presence of mice and rats. Variables associated with ABB presence were biomass of mice, catch-per-unit-effort of mice, percentage of ground cover that was forbs and grass, low overnight temperature, and month. Competition studies indicated that scavengers are far more successful than beetles in obtaining carcasses, with 89% and 50% of carcasses being scavenged in 2013 and 2014 respectively. Lastly, beetles chose rats sized 100-160 g in 32% trials examining carcass size preference.

TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION	1
II. METHODOLOGY	7
Study Area	7
Small Mammals	8
ABB Trapping	9
Habitat Analysis	11
Scavenger Study	12
Carcass Size Preference	13
Statistical Analysis	15
III. RESULTS	17
Small Mammals	17
Statistical Models	18
Habitat Characteristics	19
Scavenger Study	19
Carcass Preference	20
IV. DISCUSSION	21
LITERATURE CITED	39
APPENDICES	44

LIST OF TABLES

Table	Page
1. Model selection results for the effects of rodents, plants, soil, and abiotic conditions on the number of ABB caught per trap	28
2. Catch per unit effort (C/E) of rodents as calculated for 2013 and 2014	29
3. Percentage of carcasses scavenged or buried by beetles during scavenger study ..	30
4. Results of cafeteria-style carcass preference trials	31
5. Mean, SE, minimum and maximum values of potential explanatory variables measured at all grids to predict presence of ABB	31

LIST OF FIGURES

Figure	Page
1. American burying beetle	32
2. Habitat range in US	32
3. C/E versus ABB 2013	33
4. C/E versus ABB 2014 interior sites	34
5. Total C/E versus ABB	35
6. Habitat variables versus ABB	36-38

CHAPTER I

INTRODUCTION

The American burying beetle, *Nicrophorus americanus* (ABB) is a species of carrion beetle in the family Siphilidae (Fig. 1). Members of this genus are known as burying beetles because of the shared suite of behaviors displayed during reproduction when readying a carcass of another animal as a source of food for their offspring (Scott, 1998). Nocturnally active, ABB are the largest beetles of the genus (27-35 mm long) and are characterized by an orange to dark red frons and pronotum (Anderson, 1982; Lomolino *et al.*, 1995). Their large size allows them to manipulate larger vertebrate carcasses, thus excluding several congeners from competition. American burying beetles use a large range of sizes and types of vertebrate carcasses for feeding purposes. Conventional wisdom states that for reproductive purposes, ABB have demonstrated preference for carrion weighing between 80-100 g (Kozol *et al.*, 1988). However, a lone female ABB was documented burying a chick carcass weighing 229 g (Kozol *et al.*, 1988). Research indicates that ABBs are attracted to and capable of reproducing on a wide variety of carrion including mammals, birds, reptiles and amphibians (Kozol *et al.*, 1988, Bedick *et al.*, 1999). Highly developed chemoreceptors allow ABB to identify carrion within 24 hours of death and up to several kilometers away (Kalinová *et al.*, 2009). American burying beetles have been observed traveling distances up to 2.9 km in a single night in search of carrion (Creighton & Schnell, 1998). Competition for carrion resources is intense, as the availability of suitable carrion is

unpredictable and valuable to other animals. This competition is likely to have contributed to the development of biparental care, a rare trait among beetles (Anderson, 1982).

Typically, once the male has located a carcass, he releases pheromones via a characteristic headstand stance to attract females (Beeler *et al.*, 1999). Multiple other beetles of both sexes are attracted by the pheromones, and competition ensues until a single male and female successfully claim the carcass (Scott *et al.*, 1987). The victorious pair proceeds to cooperatively bury the carrion by excavating soil from underneath the carcass. As they bury the carcass, the beetles strip all feathers or fur, and cover it with oral and anal secretions to retard microbial growth and control decomposition. The result is a “brood ball” and serves to feed both the parents and offspring until they emerge as teneral adults. Females lay between 10-35 eggs slightly above the brood ball, where parents remain until larvae hatch (Kalinová *et al.*, 2009). While a pair of ABB usually completes this process, individual beetles have been observed burying a carcass alone. Female ABB possess the ability to cache sperm from previous mating events, which may allow for a single female beetle to bury a carcass and reproduce (Müller and Eggert, 1989). Hatched larvae are fed regurgitated bits of brood ball by both parents for 3-7 days after hatching, at which time the male leaves. The female typically remains until the larvae enter pupation, about two weeks after hatching (Scott *et al.*, 1987). Approximately one month after the carcass was buried, teneral adults emerge from the ground, over-winter in the soil, and finally join the breeding population the following summer.

American burying beetles were once considered to be widespread across North America, but were listed as endangered in 1989 by the U.S. Fish and Wildlife Service (USFWS, 2008). In the mid-19th century, ABB were documented as abundant throughout the middle and southern portion of the U.S. (LeConte, 1853). Museum specimens and field studies prior to the 1920's

reported that ABB were common across the eastern half of North America (Davis, 1980; Anderson, 1982; Sikes and Raithel, 2002). The extensive museum collection at Cornell University was examined in 1976 for ABB records, the most recent collection of the beetle was documented nearly 40 years prior (Davis, 1980). In 1980, despite trapping efforts of several individuals, a single capture in Kentucky was the only reported presence of ABB in the U.S. since 1961 (Davis, 1980). Currently, ABB occupies a fraction of its historic range, appearing to have disappeared from nearly 90% of its former habitat (Lomolino *et al.*, 1995; Creighton *et al.*, 2009). When ABB were listed as an endangered species, only two known populations existed: one on Block Island, Rhode Island, and another in Latimer County in eastern Oklahoma (Fig. 2). Since then, extant populations have been documented in 55 counties within seven other states: Massachusetts, Kansas, Ohio, Texas, Nebraska, South Dakota, and Arkansas (Kozol *et al.*, 1988; USFWS, 2012b).

The decline of ABB is not well understood, as while ABB are reportedly endangered, all eight of its sympatric congeners have experienced no apparent population decline (Sikes and Raithel, 2002). Several hypotheses have been proposed. For example, Anderson (1982) suggested that ABB were limited to areas with substantial litter and deep, loose soils characteristic of deciduous forests of eastern North America. Loose soil allows for easier burial of carrion and perhaps more favorable microhabitat. Anderson (1982) hypothesized that ABB populations have declined as a result of deforestation of these types of habitats. A recent study supported this hypothesis by demonstrating that areas of forest removal experienced significant declines in ABB populations while adjacent, undisturbed areas experienced no decline (Creighton *et al.*, 2009). Further, although ABB may be habitat generalists while searching for carrion, they are more particular when searching for an appropriate burial site (Lomolino *et al.*,

1995). However, ABB are known to exist in open grassland/non-forested areas (e.g., Rhode Island) (Lomolino *et al.*, 1995) and Osage County, OK (D. Howard, pers. comm.). Both populations (OK and RI) reside in open areas with loose, deep soil suggesting that soil type may be a determining factor in location of breeding areas rather than forest *per se*. For example, a study conducted in Oklahoma found a positive correlation between the presence of ABB and percentage of sand present in the soil (Lomolino *et al.*, 1995).

Another hypothesis regarding ABB decline is that habitat fragmentation and expanded edge habitat increases the abundance of medium sized scavengers (e.g., coyote (*Canis latrans*), American crow (*Corvus brachynchos*), and others (Sikes and Raithel, 2002.)) Release of these scavenger populations could increase competition for similar-sized carrion as used by ABB (USFWS, 1991; Holloway and Schnell, 1997; Sikes and Raithel, 2002.)

Pesticide use, specifically dichloro-diphenyl-trichloroethane (DDT), has also been proposed as an explanation for ABB population decline. DDT was widely used in the U.S. between 1940 and 1972. However, several studies have investigated this hypothesis (Hoffman *et al.* 1949; Kozol, 1988; Raithel in USFWS, 1991) and provide evidence that ABB are currently present in places where DDT had been sprayed (Sikes and Raithel, 2002); and that, populations have disappeared from places where DDT was never used. Nonetheless, Hoffman (1949) showed that several sympatric congeners of ABB were eliminated from areas as a result of the use of DDT. Although DDT use may not be the chief influence in ABB decline, in conjunction with other factors, it could explain some of the decline of this species.

A prevalent hypothesis concerning the decline is that ABB are resource-limited relative to reproductive requirements for habitat and carrion (Lomolino *et al.*, 1995). For example, studies suggest that using large carrion for reproduction results in larger broods (Kozol *et al.*,

1988). Large, optimal sized carrion are likely less abundant than other carrion (e.g. mice) and once found, likely more difficult to bury. However, data supporting an optimal carcass size for reproduction are limited and perhaps misrepresented (Amaral *et al.*, 1997; Holloway and Schnell, 1997; Lomolino and Creighton, 1996). Indeed, carcass sizes of 100-200 g are often considered optimal based on several studies; yet, Kozol *et al.* (1988) found that carcasses of 80-100 g were preferred when ABB were offered avian and mammalian carcasses ranging in size from 60-206 g. Further, the increase in brood size with increased carrion mass stems from a study where ABB were forced to use larger sized carrion (Kozol *et al.*, 1988).

Another proposed factor related to waning ABB populations is the loss of optimal sized carrion. Large-scale changes in land use may result in an overall change in small mammal populations and result in a decrease of available carcasses, thereby increasing competition for those carcasses. For example, the extinction of the passenger pigeon (*Ectopistes migratorius*) due to overhunting and deforestation of large parts of their habitat in the mid 19th century has been proposed as contributing to ABB decline (Sikes and Raithel, 2002). Populations of passenger pigeons numbered in the millions and are thought to have been a primary source of carrion for ABB (Amaral *et al.*, 1997). Holloway and Schnell (1997) investigated the relationship between ABB and available carrion by plotting the number of ABB trapped per site against the biomass of birds and mammals sized up to 200g. Their results indicated a positive correlation between ABB and mammal biomass at each site, yet their data were confounded as the beetle data was collected one year after the mammal and bird data. This hypothesis disintegrates when one considers that carcasses disappear from the landscape quickly, often within 1 day (Santos *et al.*, 2011) and beetles are adept at locating carcasses from great distances and moving to those carcasses quickly. These traits would suggest that ABB are not as reliant on local carrion

resources as some studies may suggest (Creighton *et al.*, 2009; Creighton and Schnell, 1998; Holloway and Schnell, 1997; USFWS, 1991.) Further, optimal carrion size data is somewhat spurious due in part to the design flaws of the few studies aimed at investigating the relationship. Whether an individual ABB will secure or discard a particular sized carcass when faced with random availability of carcasses of unknown size is an open question, and possibly a conditional behavior linked to beetle body size or some other factor.

There are few studies that have reported on the relationship between ABB populations and availability of vertebrate carrion (Sikes and Raithel, 2002), selection of optimal sized carrion by ABB, and competition between ABB and scavengers for carrion (Holloway and Schnell, 1997). Thus, the goals of this study are to: 1) assess the relationship between small mammal populations and ABB abundance in different habitats, including associated environmental factors, 2) assess competition for carrion between ABB and vertebrate scavengers and, 3) evaluate carrion size selection by ABB.

CHAPTER II

METHODOLOGY

Study Area. – Field portions of this study were conducted in 2013 and 2014 at the McAlester Army Ammunition Plant (McAAP) in Pittsburg County, Oklahoma. The McAAP is an 18,196 ha area owned and operated by the United States Department of Defense. The area encompasses over 1,200 ha of wetland habitat, ponds and lakes (US Army, 2015). Vegetation is characterized by 60% tallgrass prairie and 40% oak-dominated forest. Common vegetation species encountered include little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), broomsedge bluestem (*Andropogon virginicus*), panicums (*Panicum* spp.) and oaks (*Quercus nigra*, *shumardii*, *stellata*, *marilandica*). Brushy areas comprised of greenbriar (*Smilax bona-nox*), buckbrush (*Symphoricarpos orbiculatus*), winged elm (*Ulmus alata*), sand plum (*Prunus angustifolia*), sumac (*Rhus* spp.) and persimmon (*Diospyros virginiana*) punctuate the landscape (Ditchkoff *et al*, 1996; Ditchkoff *et al*, 2001; Ditchkoff *et al*, 2000; Ditchkoff *et al*, 2001). Prescribed burning is frequently used as a habitat management tool at McAAP; however, all locations used in this study had been free of fire disturbance since 2010 (B. Starry, pers. comm.). Mean annual rainfall in this area is 100.3 cm, with a high mean temperature of 32°C and a low mean temperature of 20°C during May - August. Average maximum wind speed in McAlester during the summer is 18.5 kph (Oklahoma Mesonet, 2015). Two habitat types (grassland and forest) were chosen to investigate the effect of habitat on ABB populations.

Although great effort was taken to place trapping grids in areas representative of these habitats, most often encountered in forested sites was a mosaic of closed canopy and open areas.

Grassland grids were free of a central woody component, but often flanked along the perimeter by forested areas. This patchwork of habitat results in a diverse small mammal assemblage, atypical of the species found in true closed canopy forests or savannahs.

Small Mammals. – A conventional mark-recapture study was conducted on six sets of grids (n = 12) in 2013 and 2014. Each set of grids consisted of three locations in forest interior habitat (defined as 30 meters interior to the edge of the tree line, under tree canopy), and three located in grassland habitat (characterized by prairie grasses and lack of mature woody component). Grids were separated by approximately 1 mile at the centers to ensure independence (i.e.- prevent animals from moving between grids). At each grid, 64 Sherman® folding live traps sized 7.6 x 8.9 x 23 cm (H.B. Sherman Traps Inc., Tallahassee, FL) were placed in an 8 x 8 arrangement with 15 m spacing between traps. In some cases where geographic or habitat features did not allow for an 8 x 8 grid, a 4 x 16 trap arrangement was used. Asphalt roof shingles were placed on top of traps located in direct sunlight to reduce exposure to the sun.

Trapping was conducted on a two week alternating basis, allowing three paired grids (n = 6) to be sampled simultaneously. Grids were sampled for 3 consecutive days or longer, to achieve a $\geq 80\%$ recapture rate. In cases of unfavorable weather, the trapping period was extended. Mammal traps were baited with a mixture of rolled oats and peanut butter, and opened in the evening between 17:00 and 21:00 hours. Traps were checked as early as possible (between 06:00 - 11:00 h) the following morning and the order in which they were checked was rotated

each day. For each capture, I recorded grid and trap number, species, sex, age class, weight, reproductive condition and if the individual had previously been captured. Weight was measured to the nearest 0.5 g using a Pesola® spring scale (Pesola AG, Baar, Switzerland). Age class (juvenile or adult) was determined by a combination of pelage color and body mass. Mice (*Peromyscus leucopus*, *P. maniculatus*, *P. attwaterii*, *Reithrodontomys fulvescens*) weighing ≥ 15 grams were considered adults; those ≤ 15 grams were juveniles. Rats (*Sigmodon hispidus*, *Neotoma floridana*) weighing ≤ 80 grams were classified as adults, those ≥ 80 grams as juveniles. Reproductive condition was assessed visually or by palpation, and recorded as either scrotal or non-scrotal for males; open, lactating or pregnant for females. A female was considered pregnant if embryos were detected upon palpation. Lactation was determined by the absence of fur around the nipple area. A female was considered open if not pregnant or lactating. Animals were individually identified with a metal self-piercing Monel ear tag (size #1005) displaying a unique number (National Band & Tag Company, Newport, KY). Ear tags were numbered 1-300, and in the case of repetition, an additional numbered tag was placed in opposite ear. Location and number of each tag was recorded and animals were released alive. Sprung traps (empty or those containing something other than rodents) and all incidence of trap mortality were recorded. Trapping and animal handling was conducted pursuant to standards established by the American Society of Mammalogists and under Oklahoma State University Animal Care and Use Committee protocol AS-0133.

ABB Trapping. – A single bucket trap designed to capture ABB was placed at the center of each small mammal grid. Traps consisted of a 5-gallon bucket with drainage holes drilled in the sides and bottom. A plywood lid was fitted to the top of each bucket to provide a landing pad for

beetles, and was attached to the bucket using a J-bolt assembly. The lid had a 6-inch diameter opening in the center that opened into a plastic funnel leading into the bucket. Above each opening was a plastic cover to prevent rain from directly entering the bucket. Each bucket contained 2.2 L of pre-moistened substrate (70/30 mixture of peat and sphagnum moss) as a refuge for captured beetles. Traps were baited with one rat (180-280 g) (*Rattus norvegicus*) carcass (Big Cheese Rodent Factory, Ft. Worth, TX). Each rat was aged in a sealed container for 48-72 hours prior to each trapping period. Bait was placed in a plastic container (~1200 mL) inside each bucket. A minimum of twelve 3/8-inch holes were drilled in each container to allow the scent to disperse and reduce chances of other insects coming into contact with the carcass. Each bucket trap was secured to a tree a minimum of 15cm off the ground to minimize ant access to the bait, allow moisture to drain and deter disturbance by scavengers. Trees were carefully selected so that trap placement minimized exposure to sunlight, reducing incidence of beetle desiccation.

Beetle traps were opened in conjunction with small mammal trapping. Beetle traps were opened in the evening and checked prior to 10:00 h the following morning to reduce mortality caused by heat and desiccation. All captures were identified to species, sexed, and aged. Age was determined by the time of year at capture; early season captures are typically overwintered adults while late season captures are usually newly emerged teneral beetles (USFWS, 2012). Age is also determined by observing coloration of the beetle; teneral beetles are brighter orange than older individuals, which appear more reddish or burnt orange in color (USFWS, 2012). Sex is determined by the shape of the orange marking located between the frons and the mandibles of a beetle; females exhibit a triangular shaped spot, while males have a rectangular shape (USFWS, 2012). Pronotum width (± 0.01 mm) was measured as an indicator of body size. Each ABB was

outfitted with a numbered bee tag attached to the elytra with gel glue. As an additional measure of identification, the hind orange marking of the right elytron of each beetle was branded using a cauterizing iron (Butler *et al.*, 2012). Beetles were then placed in a plastic container with a small bit of canned cat food and allowed to eat. This step served to allow the glue to dry and to potentially prevent the beetle from re-entering the bucket trap due to hunger. Beetles were released alive at site of capture. All ABB traps were removed from the grid after each trapping period in an attempt to minimize lingering bait odors. All ABB trapping was performed under USFWS ESA Section 10 (a) permit number TE 94766A-1.

Habitat Analysis. – Vegetative ground cover, tree canopy cover, tree basal area, soil texture class, soil organic matter, and herbaceous plant biomass were measured at each trapping grid. Each variable was measured once per year in July at 5 locations (the four corners and center) within each grid. Soil samples were taken at 15 locations across each grid at a depth of 15 cm. Soil samples per grid were combined and mixed, then stored in plastic bags and frozen until they could be transported to the Oklahoma State University Soil and Forage Analysis Lab for determination of texture class (% sand, clay and silt) and organic matter content. Soil was analyzed once per grid during the 2-year study. Ground cover was measured using a 1m² Daubenmire plot, and placed into categories based on composition: forbs, woody, grass, leaf cover, bare ground or rock. Categories were averaged and presented as a percentage for each grid. Canopy cover was measured using a spherical densiometer (Forestry Suppliers Inc., Jackson, MS) facing each cardinal direction. Measurements were averaged to provide a single value for each grid. Basal area was measured using a wedge prism with a basal area factor (BAF) of 10 (Forestry Suppliers Inc., Jackson, MS). Mean basal area (m²/ha) was calculated by

multiplying the number of countable trees by 10. Plant biomass was measured by cutting all vegetation inside the 1m² Daubenmire square down to ground level at the center and four corners of each grid. To avoid biasing trapping efforts, biomass samples were collected after trapping ceased in 2014 (early August). Samples were stored in plastic trash bags and refrigerated until they could be taken to drying ovens at Oklahoma State University. Samples were placed in a drying oven at 49°C for 72 hours, then weighed to the nearest gram. Biomass samples were taken at 11 grids in 2014. One grid was not included as it was mowed for hay prior to samples being taken, but after trapping efforts ceased. All data for temperature, wind speed, moon phase, and precipitation was obtained from Oklahoma Mesonet (www.mesonet.org).

Scavenger Study. – To assess competition for carcasses from vertebrate scavengers, rat carcasses were placed on the landscape and monitored for 72 hours. In July 2013, May 2014 and August 2014, 16 rat carcasses were placed on the six small mammal grids (n = 96). Carcasses were thawed for 12 hours prior to placing them on grids. Each carcass was a 180 - 279 g lab rat (*Rattus norvegicus*) (Big Cheese Rodent Factory, Ft. Worth, TX) attached to 4m of braided fishing line that was secured to a standard sewing bobbin. The bobbin was attached to a loop of wire so that it could spin freely. In forested grids, the wire loop was secured to the trunk of a tree with baling wire. In grassland areas, a 1 m length of metal rebar was hammered into the ground and served as the attachment point for the wire loop. Carcasses were assessed for signs of scavenging or beetle burial every 24 hours for 72 hours total. Carcasses were considered scavenged if eviscerated or completely gone. If the length of fishing line led into the ground, the carcass was considered buried by a beetle. If beetles were visible (i.e.- in the process of burial),

species was recorded. If beetles were not visible, no attempt was made to exhume or disturb the carcass to determine species. At the end of the 72 hours at all burial sites, the remaining length of fishing line was cut off at ground level and measured to determine burial depth (± 1 cm). I also recorded the presence of other organisms (spiders, maggots, turtles, etc.) on carcasses. At the end of the trial, all remaining carcasses were removed as to prevent odors from lingering and potentially interfering with ABB trapping.

Carcass Size Preference. – Laboratory trials were conducted to investigate if burying beetles exhibit a preference regarding the size of carcasses used for reproduction. Trials were conducted in an enclosure (3' x 3' x 5.5') constructed of plywood and plexiglass. Two sides had two 8-inch openings near the bottom fitted with a short length of plastic PVC pipe, with a removable perforated PVC cap to allow for easy access to the inside and bottom of the box. The top of the enclosure was outfitted with a small electric fan to draw air through the box to encourage scent dispersal.

Wild caught *Nicrophorus marginatus* were obtained in mixed sex colonies from generous researchers, but then separated by sex at OSU to prevent unwanted mating. Lighting was placed on a 14:10 light : dark cycle to simulate the natural photoperiod during summer, which corresponds to peak ABB activity. Beetles were housed in glass aquaria with about 2.5 cm of pine shavings and sections of cardboard egg crates for shelter. Beetles were fed canned dog food, and distilled water was provided via plastic tubes stoppered with cotton balls. I chose to work with a congeneric species for two reasons: acquiring permission to house and breed ABB was not possible at the time, and *N. marginatus* is the closest in body size to the ABB. Although *N. marginatus* are diurnal, rather than nocturnal, I felt them to be well suited for experimental

extrapolation, as the primary goal was to see how beetle body size correlated to body size of chosen carrion.

A single beetle of each sex was chosen randomly for each trial. At 24 hours prior to the start of the trial, paired beetles were placed in separate plastic containers outfitted with wire mesh lids. Only water was allowed during this time. White laboratory rats (*Rattus norvegicus*) (Big Cheese Rodent Factory, Ft. Worth, TX) were separated into four size categories based on their body weight: small (below 30 g), medium (60-80 g), large (100-160 g), and jumbo (250+ g). One rat from each size category was selected 24 hours prior to the start of the trial, and allowed to thaw at room temperature. At 12 hours prior to starting the trial, these rats were placed two inches apart on one to two inches of potting soil in the bottom of the trial chamber. The order in which they were placed was determined by random drawing of numbers before each trial. Simultaneously, the containers housing the selected beetles were moved into the bottom of the chamber, 4 inches away from the rats but directly next to each another. The lid was placed on the enclosure and the fan turned on, allowing beetles to acclimate to the scent of the carcasses. Trials began 3 hours after lights came on each morning (at 9:30 am). I released each beetle from its housing container into the trial chamber. Behavior was separated into the following categories: body size investigation, burial preparation, mating, and feeding. Body size investigation included beetles making repeated loops around a particular carcass, going underneath a particular carcass, or carcass weight determination, in which a beetle moves under a carcass and performs reverse push-ups to assess its ability to move the carcass. Burial preparations included observing beetles beginning to strip the fur from a particular carcass, or excavating soil in a burial attempt. All copulation events and attempts were recorded as mating behavior. If beetles exhibited one or more of these behaviors at or on a particular carcass, the

trial was stopped. Carcass size of selected rat and pronotum width (nearest 0.1mm) of each beetle was documented. Beetles were then removed from the trial chamber, placed together in a small aquarium filled with ~6 inches of soil and allowed to bury the selected carcass. Trials ceased at 90 minutes if no preference behavior was observed. For this investigation, 44 trials were conducted (n = 88 unique beetles).

Statistical Analysis. – Relative population abundance of small mammals was calculated for each grid on a catch-per-unit effort basis and expressed as the number of animals caught per 100 trap nights, and corrected for sprung traps by all causes (Nelson and Clark, 1973). A trap night was defined as a single trap set for a single 24-hour period (Nelson and Clark, 1973). Preliminary correlation of explanatory variables was performed using SAS 9.4 (SAS Institute, Cary, NC), and was followed by regression analysis for small mammals, scavenger study and carcass preference. Testing for multicollinearity yielded two groups of variables important to predicting ABB populations: biomass of mice + biomass of rats and catch per unit effort (C/E) + mean body weight of small mammals (BW). These groups were highly correlated to ABB and to one another; so further analysis included either biomass or C/E + BW, but not both. Remaining variables were standardized so that each had a mean of 0 and a standard deviation of 1. A Poisson distribution was used to standardize the number of beetles captured. Generalized linear mixed modeling (GLMM) was used to account for pseudo-replication created by repeated sampling of multiple grids. Individual grids were treated as random variables. Models were then analyzed using a model comparison approach in R (version 3.2; R Development Core Team, Auckland, NZ) and selected based on Akaike's Information Criterion (AIC) values (Burnam and

Anderson, 2002). To correct for finite sample size bias, the corrected AIC (ΔAIC_c) was used. Results with ΔAIC_c less than 7.0 were considered as best-fit models for each variable. Models that had ΔAIC_c greater than a simpler version of the model were also eliminated. Akaike's weighted values (w_i) were calculated for each model to indicate the weight of evidence when compared to other models (Burnham and Anderson, 2002).

CHAPTER III

RESULTS

Small Mammals. – Rat species captured in 2013 include *Sigmodon hispidus* (n = 69) and *Neotoma floridana* (n = 4). Species of mice captured included *Peromyscus maniculatus* (n = 32), *P. leucopus* (n = 58), *P. attwateri* (n = 1) and *Reithrodontomys fulvescens* (n = 34). In 2013, a positive relationship between total C/E and ABB ($r^2 = 0.51$, $P = 0.07$) was indicated (Fig. 3a). This relationship is less strong when mice ($r^2 = 0.44$, $P = 0.1$) and rats ($r^2 = 0.44$, $P = 0.1$) are separated, but the association is still evident (Fig 3b and c). Due to the small sample size for 2013 (6 grids versus 12 in 2014) results for this 2013 are not separated by habitat type. A total of 33 ABB were captured in 2013, with 24 captured in grasslands and remainder in forested locations. Beetles captured at forested sites averaged 10.0 ± 0.8 mm, while those found in grasslands averaged 9.3 ± 0.6 mm (Table 2).

I analyzed relationships between ABB and rodents separately between forest and grassland habitat in 2014. Rat species captured in 2014 included *Sigmodon hispidus* (n = 399) and *Neotoma floridana* (n = 28). Most of the rats captured at interior grids were *N. floridana* (n = 28), but *S. hispidus* was also found (n = 15). There were no *N. floridana* captured at grassland sites, but 384 *S. hispidus* were captured. Mice species captured include *Peromyscus maniculatus* (n = 290), *P. leucopus* (n = 672), *P. attwateri* (n = 51) and *Reithrodontomys fulvescens* (n =

144). A total of 128 individual beetles were captured in 2014 (62 in forested sites, 66 in grasslands; Table 2). Average pronotum width for beetles captured at forested sites was 9.7 ± 1.2 mm; those at grassland sites averaged 9.9 ± 0.9 mm. Numbers of rats and ABB captures at forest interior sites were negatively related ($r^2 = 0.55$, $P = 0.06$; Fig 4b), but no relationship existed between total C/E and C/E mice to ABB in forest sites (Fig. 4a and c). In grassland sites, rat numbers were not related to ABB, nor was total C/E (Fig. 5a and 4a, respectively). However, C/E of mice explained 41% of the variation in ABB captures ($P = 0.12$; Fig. 5c).

Combining capture data from both years allows us to identify broad trends and yields a positive relationship between ABB presence and total C/E ($r^2 = 0.43$, $P = 0.002$), although only 43% of this variation is explained. Comparing C/E for mice and rats to ABB presence separately shows that rat C/E is exerting the greater effect on ABB numbers ($r^2 = 0.23$, $P = 0.03$) compared to mice ($r^2 = 0.18$, $P = 0.07$) (Fig. 6(a-c)). Total catch per-unit-effort data indicates that mice inhabit grassland sites in higher proportions than forest interior areas (5.3 ± 2.0 versus 0.6 ± 0.2 mice caught per 100 trap nights, respectively). Rats were captured more often in grassland locations than in forested areas (10.3 ± 2.0 versus 5.2 ± 0.9 rats per 100 trap nights; Table 2). Over both years, total captures included *S. hispidus* ($n = 468$), *N. floridana* ($n = 32$), *P. maniculatus* ($n = 322$), *P. leucopus* ($n = 730$), *P. attwateri* ($n = 52$), and *R. fulvescens* ($n = 178$). All species captured were found in higher numbers at forest interior sites with the exception of *S. hispidus* and *R. fulvescens*, which were more abundant in grasslands for both years.

Statistical Models. – The most complicated models regarding ABB captures included either biomass (rats and mice) or body weight (BW) + catch per unit effort (C/E) and all of the following: month, low average temperature, overnight precipitation, probability of being

scavenged, maximum overnight wind speed, moon illumination percentage, percent of soil that was clay, percentage of ground cover that was grass and forbs. Of the 28,161 models produced, three met the AIC value cutoff of 7.0 or lower (Table 1). Models strongly demonstrated that more ABB were captured as overnight low temperature increased and as months increased from May to August. The best candidate model (although the top two models are nearly tied) strongly indicates that ABB captures increased with increasing number of mice captures and as grass and forb percentage increased ($w_i = 0.46$). Presence of rats (biomass or C/E + BW) was not represented in any of the top models.

Habitat Characteristics. — Soil composition was not a good predictor of ABB abundance, as percentage of sand in the soil ($r^2 = 0.001$, $P = 0.9$; Fig. 7a) explained less than 1% of ABB captures. Further, neither clay ($r^2 = 0.03$, $P = 0.5$, Fig. 7b) nor silt percentage ($r^2 = 0.02$, $P = 0.6$, Fig. 7d) explained ABB numbers. Organic matter did not influence ABB presence ($r^2 = 0.02$, $P = 0.7$; Fig. 7e). Mean basal area was negatively associated with beetle abundance, but not significantly so ($r^2 = 0.15$, $P = 0.6$; Fig. 7c). None of the remaining ground cover variables were significantly correlated to beetle presence, including grass ($r^2 = 0.05$, $P = 0.4$), bare ground ($r^2 = 0.11$, $P = 0.2$; Fig. 7h), rock ($r^2 = 0.02$, $P = 0.6$; Fig. 7i), leaf cover ($r^2 = 0.02$, $P = 0.6$; Fig. 7j), forbs ($r^2 = 0.08$, $P = 0.2$; Fig. 7k), woody plants ($r^2 = 0.03$, $P = 0.5$; Fig. 7l) and plant biomass ($r^2 = 0.13$, $P = 0.2$, Fig. 7m).

Scavenger Study. — In 2013, scavengers removed 85% ($\bar{x} = 13.7 \pm 1.4$) of total available carcasses within 72 hours. A single burial by beetles was observed at a forest interior site. In 2014, 13 of 192 total carcasses were buried and 50% ($\bar{x} = 8.0 \pm 2.4$) were scavenged. Over both

years, more carcasses were scavenged from forest interior sites (71%, $\bar{x} = 11.3 \pm 2.0$) than at grassland locations (52%, $\bar{x} = 8.3 \pm 2.3$). Overall, beetles were successful in burying carcasses twice as often at interior sites than at grassland grids (11 burials vs. 4, respectively).

Carcass Preference. – Out of 43 total trials, 14 resulted in beetles selecting a carcass, and 7 instances in which beetles were observed feeding on the carcass only. In the remaining 22 trials, no behavior indicative of reproduction, carcass selection or feeding was observed. When selection occurred, 8 large (100 – 160 g), 4 medium (60 – 80 g) and 2 small (< 30 g) rats were chosen for reproduction (Table 4). Beetles that selected large sized rats had a mean pronotum width of 9.1 ± 0.2 mm and those that chose medium rats had an average pronotum width of 8.7 ± 0.3 mm. Mean pronotum width of beetles that chose small rats was 8.4 ± 0.1 mm. In 3 instances, a single female beetle displayed carcass preparation behavior alone, despite the presence of a male in the chamber.

CHAPTER IV

DISCUSSION

Resource availability is one of the primary factors limiting species distributions and population densities. American burying beetle populations rely on an abundant source of small carrion to feed and reproduce; therefore, ABB are often found in areas with large small mammal populations (Holloway and Schnell 1996). Here, I investigated the influence that small mammal populations have on ABB densities in Oklahoma grasslands and forests to better understand why ABB populations and distributions are declining throughout North America. I hypothesized that ABB densities would be correlated with rat population density, as rats often fall within the range of 80 – 100 g, which is considered to be the optimal carcass size for ABB reproduction (Kozol et al. 1988). However, I instead found that the abundance of mice (<30g), which are below the optimal carcass size for reproduction, were a better predictor of ABB densities based on model selection results. However, both rats and mice were relatively good predictors of ABB based on regressions. Rat/ABB coefficients may have been leveraged by a few grids with high numbers of rats, compared to mouse abundances that were more evenly distributed over their range. Although ABB may not typically utilize mice for reproductive purposes, they will feed on carrion of any size. American burying beetles can fly long distances to actively search for carrion (Kalinová, 2009), so an abundance of mice would provide a reliable food source for beetles, while they pursue larger carrion for reproduction.

American burying beetle brood weight and number of teneral is dictated by carcass size (Wilson and Fudge, 1984). American burying beetles, like many animal species, make reproductive tradeoffs in which they either produce many small larvae when resources are abundant and a few large larvae when resources are scarce (Wilson and Fudge, 1984). Because mouse carcasses are substantially smaller than the desired carcass size proposed by Kozol *et al.* (1988), beetles in areas dominated by mice will have fewer offspring than in areas dominated by rats, assuming the ABB are restricted to these sites. While we found an abundance of small mammal resources for ABB, the lack of larger small mammals (e.g., rats) may limit the number of offspring being produced. This hypothesis is tenuous, however, as it assumes a lack of mobility by ABB.

In addition to being used as a food or a reproductive resource, the presence of rodents could secondarily affect burying beetle populations by providing abandoned burrow holes in which to rear a successful brood (Smith *et al.*, 2000). Abandoned burrows, cracks or other holes in the ground located within 20 cm of the carcass were more likely to be used for a burial, and the number of successful broods was higher for carcasses buried in the holes (Smith *et al.*, 2000). Therefore, the correlation observed in this study between C/E of mice and ABB presence may be a function of these habitat features as well as food.

Creighton *et al.*, (1993) found ABB to be more plentiful in oak-hickory forests than grasslands, suggesting that forested locations are more typical of the habitat inhabited by ABB prior to their decline. However, Lomolino *et al.* (1995) investigated the habitat affinity of the ABB in relation to food resources, and found the beetle in a wide range of available habitat types. A later study by Lomolino & Creighton (1996) reported ABB populations were distributed more in forested sites than in clear-cuts, and they found breeding success rates to be higher in

mature forest sites. I captured 90 ABB at grasslands versus 71 ABB in forested grids, an inconclusive difference between habitats. Further, I did not find a relationship between soil composition and ABB presence. My expectations were that sand would have a highly significant relationship to beetle captures, as carcasses are more easily buried in sand. Lomolino *et al.* (1995) found that ABB trapping success increased as percentage of sand in the soil increased, suggesting that ease of burial may be more influential than proximity to small mammal populations. The results indicated that ABB avoided soils that had less than 40% sand, and more than 50% silt and 20% clay (Lomolino *et al.*, 1995). Additionally, sand does not retain water well, which does not bode well for the desiccation-prone ABB. Muths (1991) suggested that burying beetles favor burial sites with added structural bulk over those comprised of only plain soil. Increased structural bulk provides stability to the brood chamber, which is essential for successful reproduction. I found that ABB density was associated with grass and forb cover, which could support Muth's hypothesis of structured bul. Habitat selection is likely driven by multiple factors including soil texture, structure, etc.

Non-carrion vertebrates can influence ABB in a variety of ways, and I found that vertebrate scavengers outcompeted ABB for carrion resources. DeVault *et al.* (2003) found that in 75% of cases, vertebrate scavengers were responsible for consuming carcasses present in a landscape. Indeed, competition for carcasses and direct predation of beetles likely hinder ABB reproduction and survival. Scavengers such as opossums (*Didelphis virginianus*) feed not only on carrion, but also directly on ABB (Jurzenski and Hoback, 2011). Also known to prey on ABB are blue jays (Bedick *et al.*, 1999), bats (Walker and Hoback, 2006), shrews (Wyatt Hoback, pers. comm.), and leopard frogs (Jurzenski and Hoback, 2011). There have been few

investigations into predation of Silphid beetles; and Young (2014) concluded that incidence of predation on carrion beetles is considerably underestimated.

Competition for carcasses may also come in the form of other insects, microbes and decomposers. The activity level of these organisms is heightened in warm months (DeVault *et al.*, 2003), which coincides with peak ABB activity. American burying beetles (as well as scavengers) must be able to locate carcasses before bacterial and fungal organisms; as toxic compounds from these organisms degrade carrion, its biological worth consequently decreases (DeVault *et al.*, 2003). I found that carcasses placed in forested sites were scavenged at a higher rate than those placed in grassland sites. The open canopy of grassland areas often experiences higher surface temperatures than forested areas, which increases the speed of decomposition. Ants, flies and other invertebrate competition subsequently increase, eventually rendering the carcass unusable for reproduction by beetles. Burying beetles enjoy a mutualistic relationship with phoretic mites carried on their bodies that consume carrion fly eggs on carcasses (Springlett, 1968). Effectiveness of mites is greatly increased if they reach eggs prior to their hatching, which is exacerbated by warmer temperatures (Springlett, 1968). In this situation, the carcass is exploited to the point that beetles will abandon burial attempts (Trumbo, 1990). During this study, carcasses that were not buried or scavenged within 48 hours were typically besieged with fly larvae and ants. On a few occasions burying beetles were observed feeding on carrion heavily inundated by maggots, but a burial was never observed after this point in decomposition.

I did not investigate whether a correlation exists between ABB presence and time since last landscape disturbance (i.e.- fire, agricultural use, mowing, etc.). Various disturbances create habitat of varying successional stages. Future research should consider type, frequency, and intensity of disturbance in areas known to sustain ABB populations. Fire as a management tool is

of particular interest. Although fire is natural to the ecosystem, prescribed fire is used as a management tool in many areas where ABB are found. Due to the over-wintering behavior of ABB, an unplanned fire could potentially decimate localized populations even if used during cool months. A study concerning the impact of regular, low-intensity fire on invertebrate populations found that the number of litter dwelling species decreased by 41-82% with this management practice. Observed effects were due to a decrease in litter layer and a reduction of associated moisture levels (York, 1999). Burying beetles are especially prone to desiccation; a laboratory study by Bedick, *et al.*, (2005) observed that beetles lose 1-5% body mass per hour in low humidity conditions, which resulted in a 50% mortality rate within 7-16 hours at temperatures between 60-82° F (Bedick *et al.*, 2005). Jurzenski *et al.*, (2014) found a negative correlation between increasing average temperature and ABB captures in Nebraska. Bedick *et al.*, (2005) suggests that this trend may be due to beetles employing behavioral tactics including avoidance of activity during the hottest parts of the day. The outcome of my study did not support those findings, instead revealing increased ABB captures as the months and temperature increased. An additional area warranting further exploration lies in soil temperature. Literature indicates that soil temperatures are higher in areas with increased edge habitat due to increased radiation resulting from less canopy cover (Van Dyke, 2008). Increased soil temperatures require beetles to bury their carcasses more quickly than in cooler months, to secure the resource before it is inundated with insect larvae (i.e., maggots), at which point the carcass is no longer usable by ABB from a reproductive standpoint. The ability of the carcass odor to disperse is greater on warmer days. Hence, it is vital that beetles are able to quickly bury to prevent scavengers from stealing an unsecured carcass. Rapidly burying a carcass, combined with antimicrobial secretions, also allow ABB to control carcass decomposition and inevitable maggot infestation.

ABB are vulnerable to a host of environmental factors. In Oklahoma, populations have remained intact while areas of former habitat elsewhere no longer sustain beetles. While I investigated multiple factors and combinations thereof, I suspect that ABB persist in areas where plentiful feeding and reproductive resources exist. Traveling to find reproductive resources is not an obstacle for ABB; reaching carcasses of optimal size, in areas of suitable soil for burial, before competitors may indeed be the regulating force for these illusive invertebrates.

Table 1. Model selection results for the effects of rodents, plants, soil, and abiotic conditions on the number of ABB caught per trap. Models with a ΔAIC_c greater than 7 and models with that had a ΔAIC_c greater than a simpler version of the model were all eliminated. We only show the explanatory variables that were supported by one of the remaining models.

H_0	ΔAIC_c	w_i	df	CE^m	forbs	grass	temp	month
H1	0	0.46	7	0.26	0.24	0.25	0.32	0.25
H2	0.001	0.46	4				0.31	0.21
H3	3.39	0.08	3				0.30	

Model variables included: mean body weight of mice (bw^m), number of mice captured per unit effort (CE^m), percent ground cover comprised of forbs (forbs) and grass (grass), minimum overnight low (temp) and month of trapping (month). Additional explanatory variables were included in the analysis but did not show up in results. These variables include: total biomass of mice or rats, number of rats captured per unit effort, mean body weight of rats and mice, the rate at which rats were scavenged in the grid and the interaction of the scavenged rate with each of the rodent factors, maximum overnight wind speed, maximum overnight precipitation, moon illumination percentage, and percent of soil that was clay.

Table 2. Catch-per-unit effort (C/E) of rodents as calculated for 2013 and 2014. Adjustments were made for traps sprung due to all causes. Adjusted weight removes sprung traps from overall capture effort for half of the time traps were open over a trapping period. Values are presented as animals captured per 100 trap-nights (TN). Total number of ABB captured and mean pronotum width in millimeters (PW) are also presented.

Grid	C/E Total	C/E Rats	C/E Mice	# ABB	\bar{x} PW
Interior					
2013					
2	2.7	0.4	2.3	1	--
7	3.9	0.4	3.5	5	9.2
8	5.3	0.4	4.9	3	9.9
2014					
1	12.0	1.5	10.5	3	10.5
2	12.4	0.4	12.0	14	9.4
3	11.1	0.3	10.8	16	9.2
7	21.6	1.3	20.3	11	9.6
8	17.3	0	17.3	12	9.7
9	12.4	0.9	11.5	6	10.0
Grassland					
2013					
10	8.3	4.3	4.0	4	10.3
11	12.7	6.7	6.0	12	10.0
13	3.9	0.6	3.3	8	10.1
2014					
4	6.5	1.4	5.1	9	9.9
5	24.7	13.2	11.5	13	10.2
6	2.8	1.7	1.1	1	--
10	6.9	2.1	4.8	12	9.7
11	24.0	17.1	6.8	20	9.7
12	5.0	0.7	4.4	11	9.8

Table 3. Percentage of carcasses scavenged or buried by beetles during scavenger study in 2013 and 2014. Each trial consisted of 16 rat carcasses (180 – 279 g) placed within the corresponding small mammal trapping grid. Trials took place on 6 grids at once, and were conducted in July 2013, May 2014 and August 2014.

Grid	# buried	# scavenged	Buried (%)			Scavenged (%)		
			24 hr	48 hr	72 hr	24 hr	48 hr	72 hr
Interior								
2013								
2	0	15	0	0	0	0	75	94
7	0	15	0	0	0	13	94	94
8	1	15	6	6	6	6	94	94
2014								
1	0	16	0	0	0	19	38	100
2	0	16	0	0	0	31	88	100
3	7	0	0	38	44	0	0	0
7	1	8	6	6	6	19	50	50
8	1	4	0	6	6	6	25	25
9	0	13	0	0	0	31	81	81
Grassland								
2013								
10	0	16	0	0	0	6	81	100
11	0	6	0	0	0	0	25	38
13	0	15	0	0	0	6	88	94
2014								
4	0	16	0	0	0	31	100	100
5	2	14	0	13	13	82	88	88
6	2	6	0	13	13	0	13	38
10	1	0	0	6	6	0	0	0
11	0	1	0	0	0	6	6	6
12	0	1	0	0	0	0	6	6

Table 4. Results of cafeteria-style carcass preference trials (n = 43). Size categories were defined as: small (< 30g), medium (60-80 g), large (100-160 g) and jumbo (250+ g). Also included is mean pronotum width in millimeters (\bar{x} PW) of beetles that exhibited preferential behavior.

Carcass Size	# chosen	success rate (%)	\bar{x} PW
Small	2*	4.5	8.4 \pm 0.1
Medium	4*	9.1	8.7 \pm 0.3
Large	8*	18.2	9.1 \pm 0.2
Jumbo	0	0	--

* Indicates inclusion of a trial in which a single female beetle displayed preferential behavior, despite the presence of a male in the chamber.

Table 5. Mean, SE, minimum and maximum values of potential explanatory variables measured at all grids to predict presence of ABB.

Explanatory variables	Mean	SE	Minimum	Maximum
Biomass mice (bm ^m)	1510.8	997.3	219	3236
Biomass rats (bm ^r)	3616.4	5241.2	0	15,847
C/E mice (CE ^m)	7.8	5.3	1.1	24.7
C/E rats (CE ^r)	3.0	4.8	0	17.1
Mean body weight mice (BW ^m)	16.1	3.5	11.5	26.5
Mean body weight rats (BW ^r)	102.1	51.6	15	300
Percent clay in soil (clay)	15.6	7.3	5.0	27.5
Percent grass cover (grass)	49.7	25.3	7.0	84.0
Percent forb cover (forb)	21.4	18.9	0	73.0
Minimum overnight temperature (temp)	66.7	5.22	54.0	76.0
Maximum daily wind speed (wind)	21.0	7.2	11.3	41.0
Moon illumination phase (moon)	44.1	32.1	0	100.0
Total daily precipitation (precip)	0.2	0.7	0	4.3
Probability of being scavenged	0.3	0.25	0	0.6
Month of trapping (month)	--	--	--	--



Figure 1. An American burying beetle (ABB), *Nicrophorus americanus*, captured at a site on the McAlester Army Ammunition Plant in McAlester, Oklahoma in June 2013.

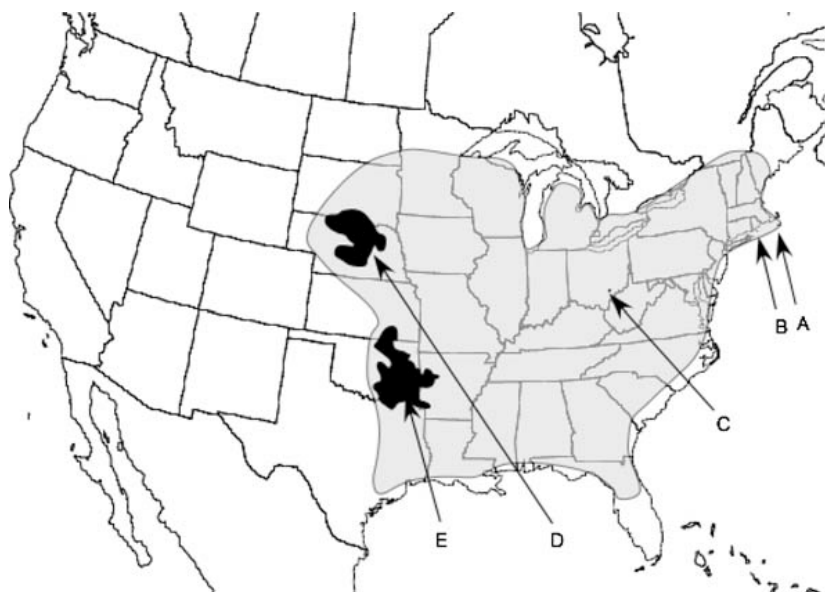


Figure 2. Distribution of ABB populations as of 2008 (black) and historic range (gray) in the United States (Creighton et al. 2009, as modified from Lomolino et al. 1995 and USFWS 1991). Letters A and C indicate areas of reintroduction attempts; B, D and E are extant populations.

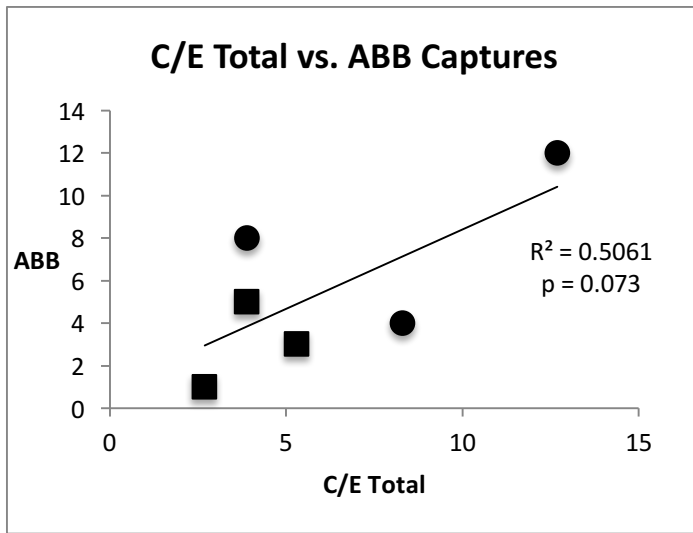


Figure 3 (a).

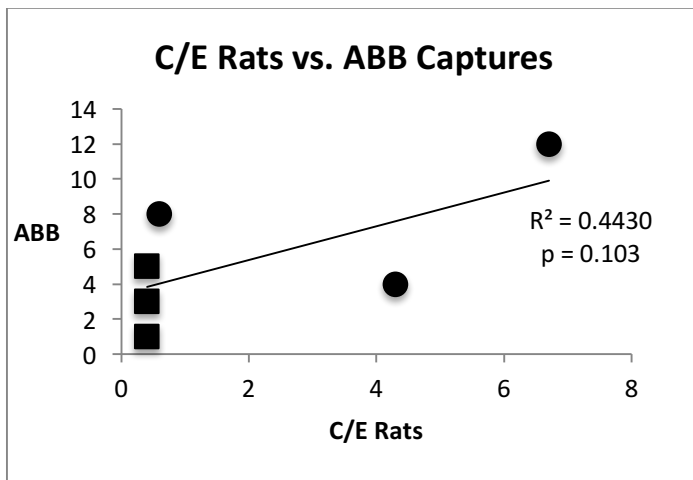


Figure 3 (b).

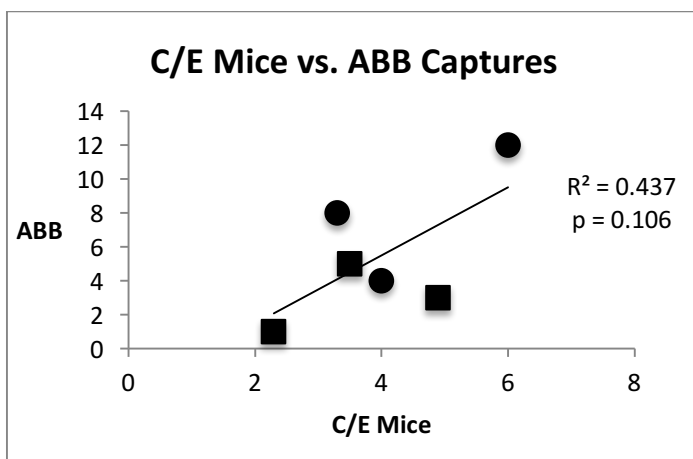


Figure 3 (c).

Figure 3 (a-c) illustrates the regression relationship between (a) total, (b) rats and (c) mice catch-per-unit-effort and ABB captures in 2013. Catch per unit effort is expressed as number of animals captured per 100 trap nights. Data points represented by a circle are grassland sites, squares represent forest interior sites.

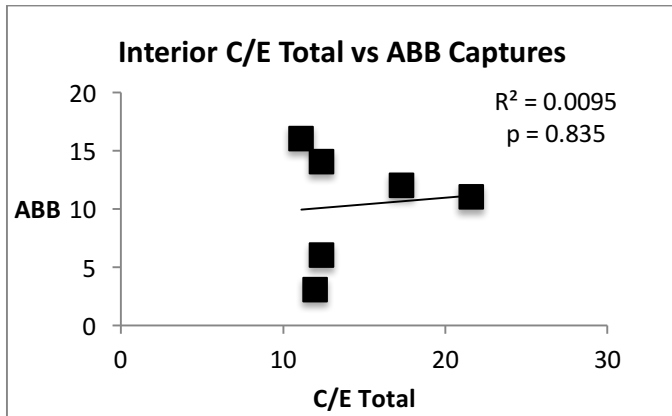


Figure 4 (a).

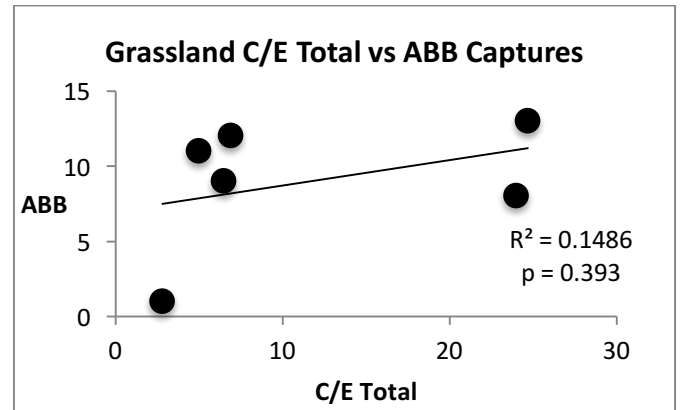


Figure 5 (a).

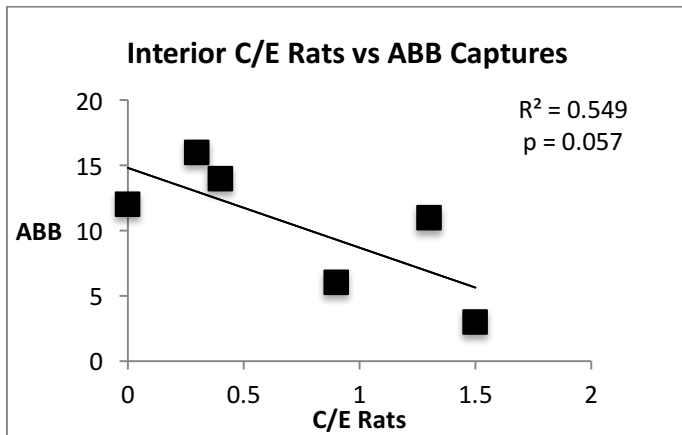


Figure 4 (b).

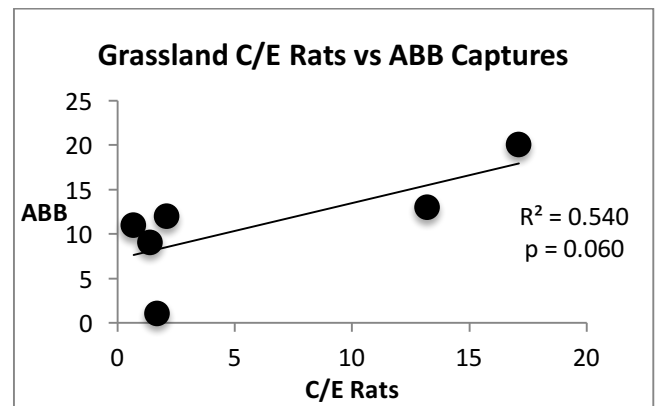


Figure 5 (b).

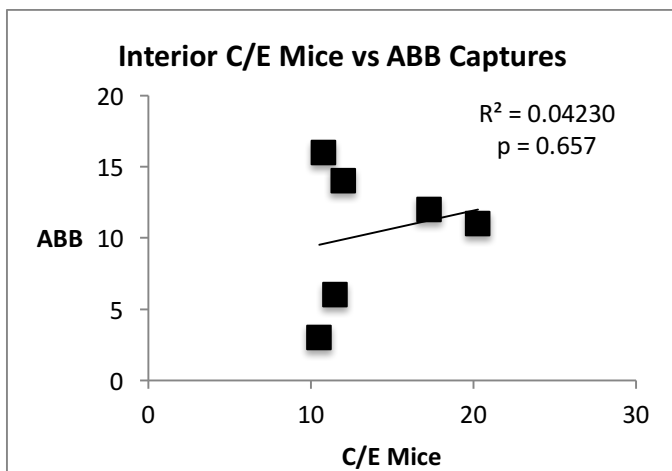


Figure 4 (c).

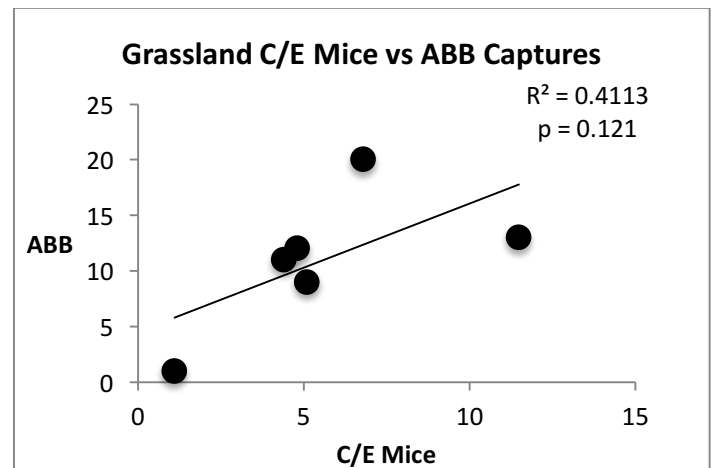


Figure 5 (c).

Figures 4 and 5 illustrate the relationship between total (a), rats (b), and mice (c) catch per unit effort and total ABB captures at McAAP forest interior and grassland grids, respectively, in 2014. Catch per unit effort is expressed as number of animals captured per 100 trap nights.

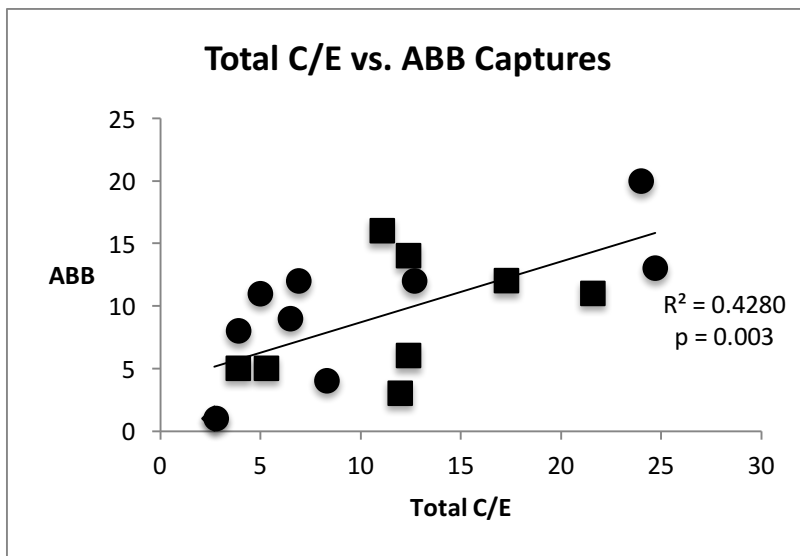


Figure 6 (a).

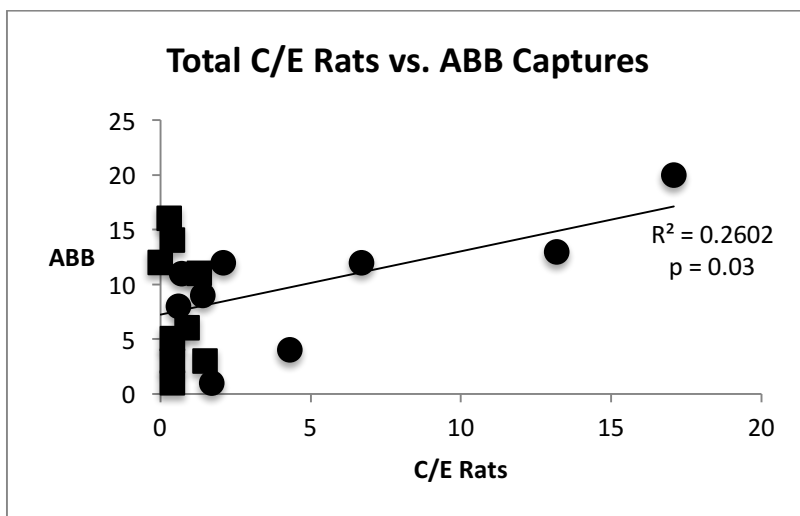


Figure 6 (b).

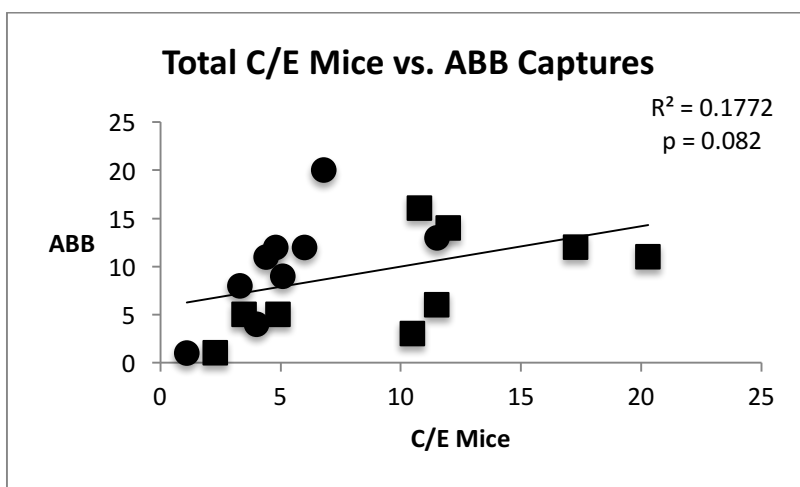


Figure 6 (c).

Figure 6 (a-c) illustrates the relationship between total (a), rats (b) and mice (c) catch-per-unit-effort and total ABB captures across all habitat types over both years. Catch per unit effort is expressed as number of animals captured per 100 trap nights. Data points represented by squares correspond to forest interior sites, and circles represent grassland locations.

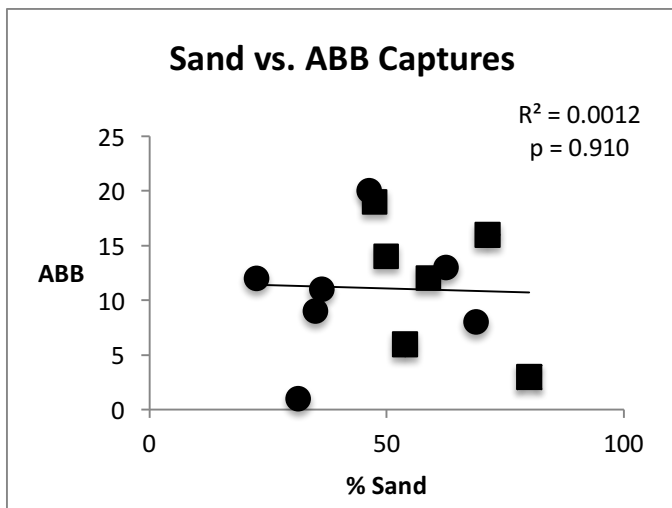


Figure 7 (a).

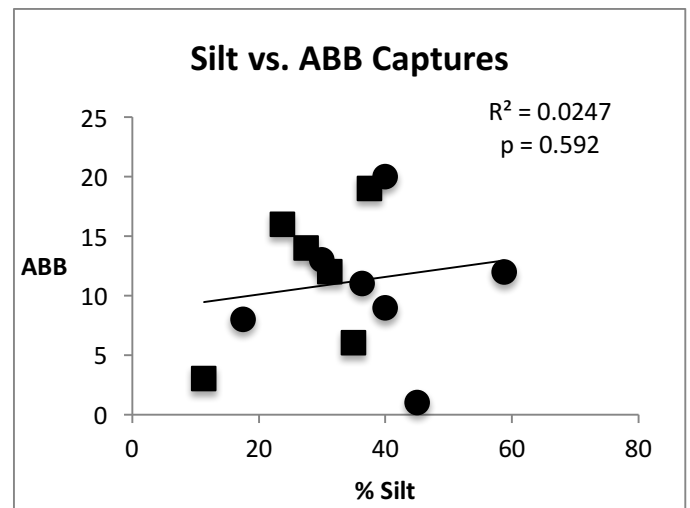


Figure 7 (d).

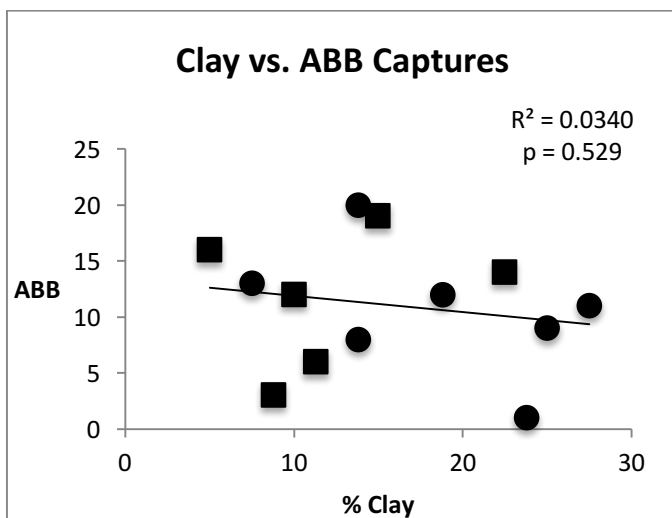


Figure 7 (b).

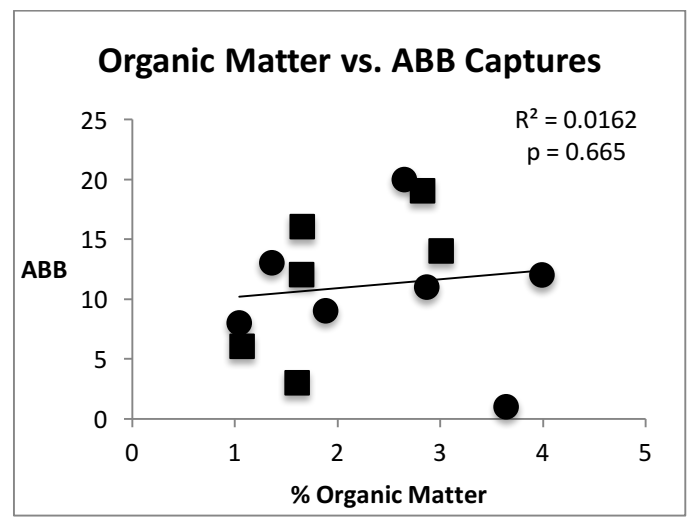


Figure 7 (e).

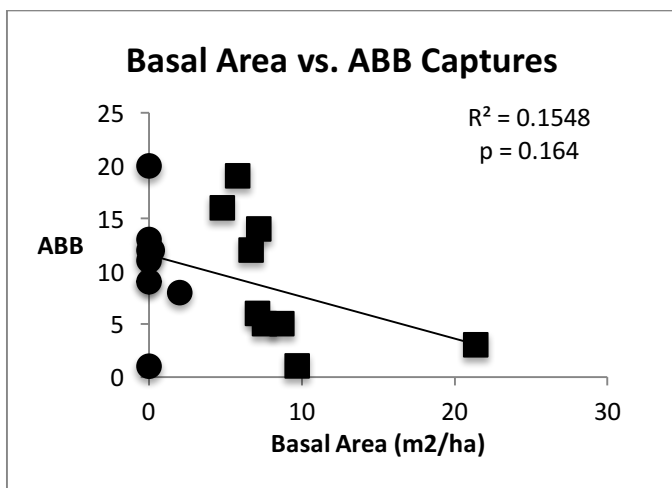


Figure 7 (c).

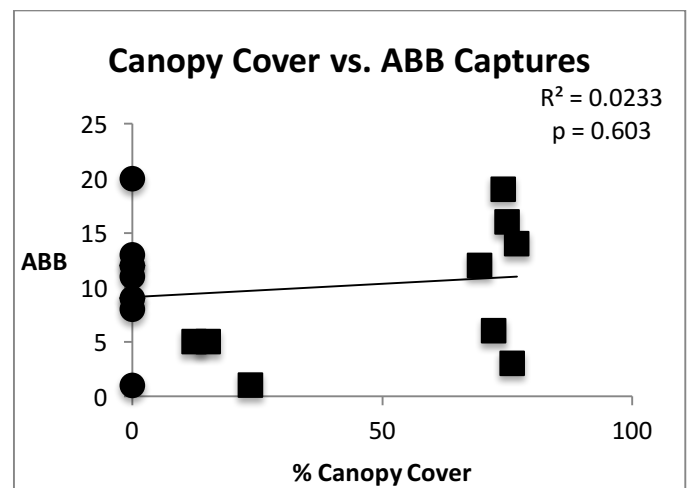


Figure 7 (f).

Figure 7 (a-m) illustrates the relationship between various habitat characteristics and ABB captures. All figures include 2013 and 2014, with the exception of plant biomass (Figure 7(m)). Plant biomass was only measured in 2014. Data points represented by squares correspond to forest interior sites, and circles represent grassland locations.

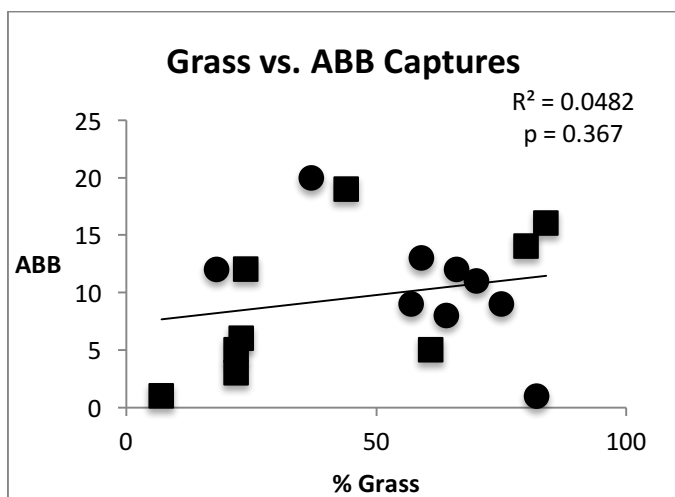


Figure 7 (g).

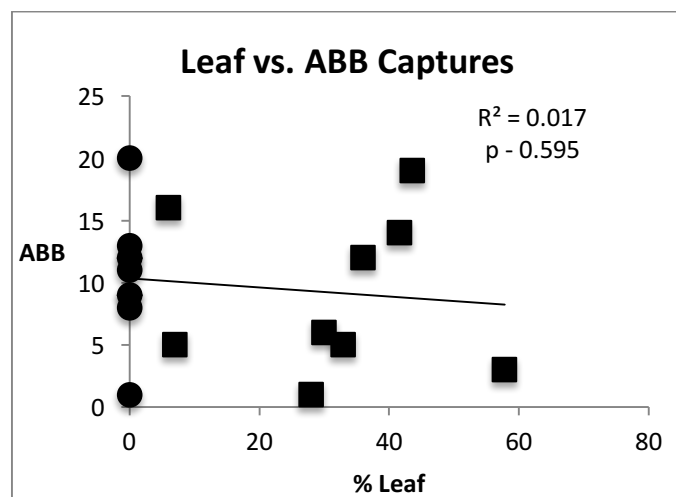


Figure 7 (j).

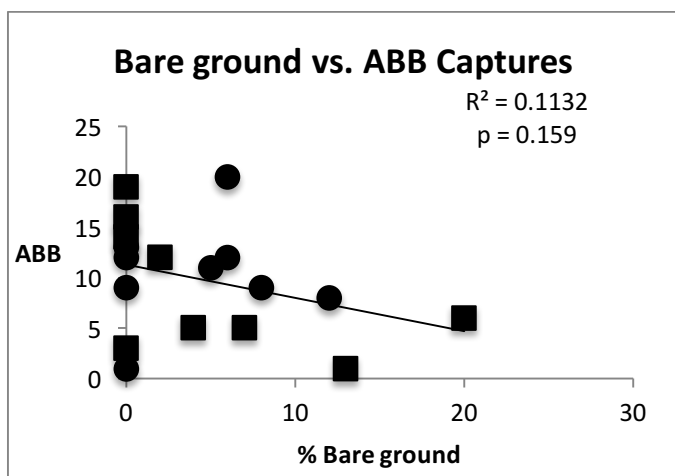


Figure 7 (h).

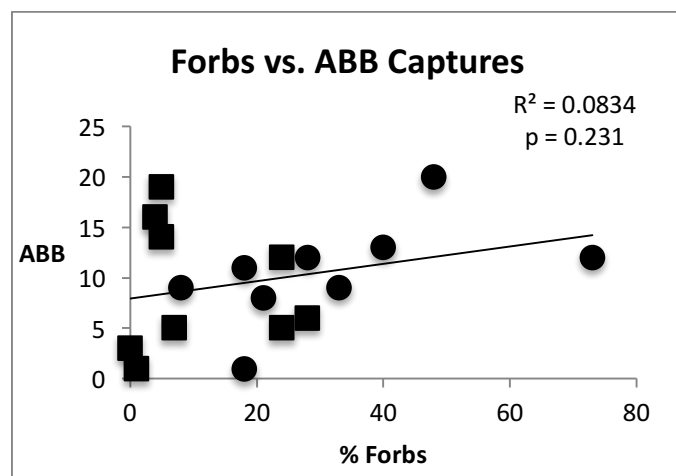


Figure 7 (k).

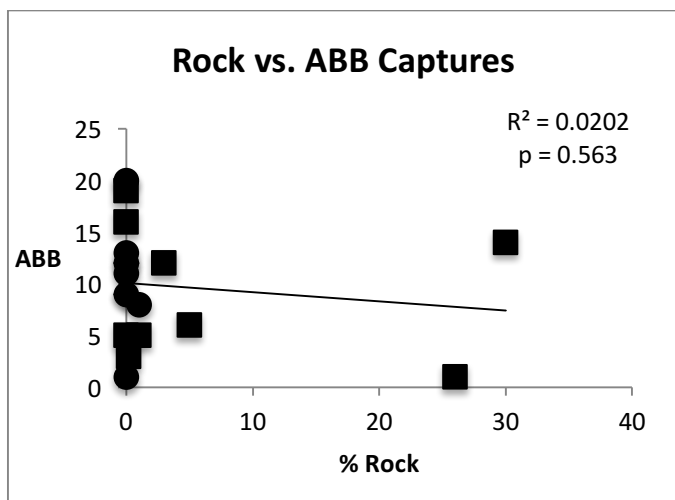


Figure 7 (i).

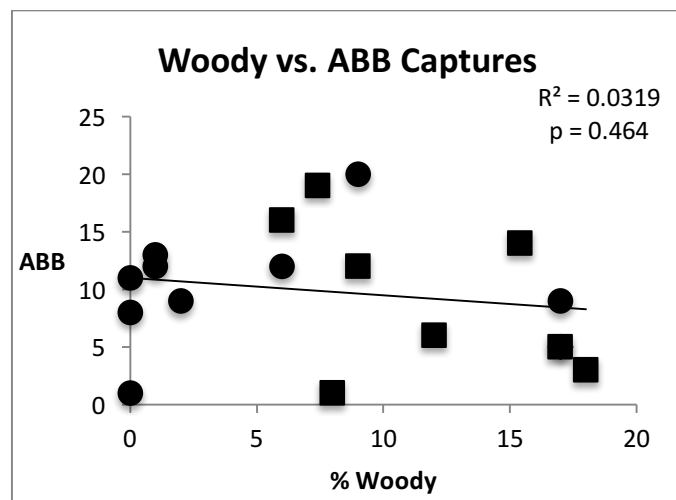


Figure 7 (l).

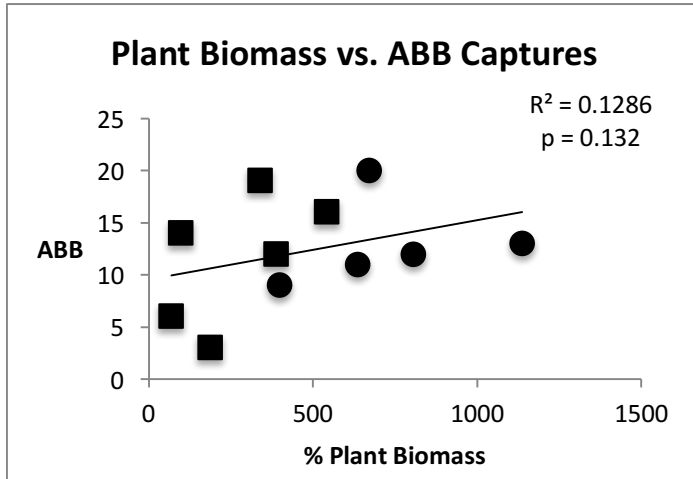


Figure 7 (m).

Figure 7 (a-m) illustrates the relationship between various habitat characteristics and ABB captures. All figures include 2013 and 2014, with the exception of plant biomass (Figure 7 (m)). Plant biomass was only measured in 2014. Data points represented by squares correspond to forest interior sites, and circles represent grassland locations.

LITERATURE CITED

- Amaral, Michael; Kozol, A; and French, T. (1997). Conservation status and reintroduction of the endangered American burying beetle. *Northeastern Naturalist*, 4(3): 121–132.
- Anderson, R. S. (1982). On the decreasing abundance of *Nicrophorus americanus* Olivier (Coleoptera: Silphidae) in eastern North America. *The Coleopterists Bulletin*, 36(2): 362–365.
- Bedick J.C., Ratcliffe B.C., Hoback W.W. and Higley L.G. (1999). Distribution, ecology, and population dynamics of the American burying beetle *Nicrophorus americanus* Olivier (Coleoptera, Silphidae) in south-central Nebraska, USA. *Journal of Insect Conservation*, 3: 171–181.
- Bedick, J. C., Ratcliffe, B. C., and Higley, L. G. (2004). A new sampling protocol for the endangered American burying beetle, *Nicrophorus*. *The Coleopterists Society*, 58(1): 57–70.
- Beeler, A.E., C.M. Rauter and Moore, A.J. (1999). Pheromonally mediated mate attraction by males of the burying beetle *Nicrophorus orbicollis*: Alternative calling tactics conditional on both intrinsic and extrinsic factors. *Behavioral Ecology*, 10: 578-584.
- Blouin-Demers, G. & Weatherhead, P.J. (2000). A novel association between a beetle and a snake: parasitism of *Elaphe obsoleta* by *Nicrophorus pustulatus*. *Ecoscience* 7: 395–397.
- Burnam, K.P. and Anderson, D.R. (2002). Model Selection and multimodal inference: A practical information-theoretic approach. New York, Springer-Verlag. 488pp.
- Butler, S.R., Jurzenski, J., and Hoback, W.W. (2012). Evaluation of marking techniques, marking retention, and mark mortality in burying beetles (Coleoptera: Silphidae). *Coleopterists Bulletin* 66: 149-154.
- Crawford, P. H. C., and Hoagland, B. W. (2010). Using species distribution models to guide conservation at the state level: the endangered American burying beetle (*Nicrophorus americanus*) in Oklahoma. *Journal of Insect Conservation*, 14(5): 511–521.
- Creighton, J. C., Bastarache, R., Lomolino, M. V., and Belk, M. C. (2009). Effect of forest removal on the abundance of the endangered American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae). *Journal of Insect Conservation*, 13(1): 37–43.
- Creighton, J. C., and Schnell, G. D. (1998). Short-term movement patterns of the endangered American burying beetle *Nicrophorus americanus*. *Biological Conservation*, 86(3): 281–287.
- Davis L.R. Jr. (1980). Notes on beetle distributions, with a discussion of *Nicrophorus americanus* Olivier and its abundance in collections (Coleoptera: Scarabaeidae,

- Lampyridae, and Silphidae). *Coleopterists Bulletin* 34: 245–251.
- DeVault, T.L., Rhodes Jr., O.E., and J.A. Shivik. (2003). Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, 102 (2): 225–234.
- Dickman, C. R., Mahon, P. S., Masters, P. and Gibson, D. F. (1999) . Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research* 26: 389–403.
- Ditchkoff, S. S., Lochmiller, R. L., Masters, R. E., Starry, W. R., and D. M. Leslie, J. (2001). Does fluctuating asymmetry of antlers in white-tailed deer (*Odocoileus virginianus*) follow patterns predicted for sexually selected trait. Proceedings of the Royal Society of London. Series B: *Biological Sciences*, 268(1470): 891-898.
- Ditchkoff, S., Welch, E. J., and Lochmiller, R. (2000). Using cast antler characteristics to profile quality of white-tailed deer *Odocoileus virginianus* populations. *Wildlife Biology*, 6(1): 53-58.
- Ditchkoff, S. S., Welch Jr, E. R., Lochmiller, R. L., Masters, R. E., Dinkines, W. C., and Starry, W.R. (1996). Deer harvest characteristics during compound and traditional archery hunts. In *Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies* 50: 391-396.
- Ditchkoff, S. S., Lochmiller, R. L., Masters, R. E., Hoofer, S. R., and Ronald A. Van Den Bussche. (2001). Major-Histocompatibility-Complex-Associated Variation in Secondary sexual traits of White-Tailed deer (*Odocoileus virginianus*): Evidence for Good-Genes Advertisement. *Evolution*, 55(3): 616-625.
- Geier, A. R., and Best, L. B. (1980). Habitat selection by small mammals of riparian communities: Evaluating effects of habitat alterations. *The Journal of Wildlife Management*, 44(1): 16-24.
- Hocking, M.D., Ring, R. A., and Reimchen, T. E. (2006). Burying beetle *Nicrophorus investigator* reproduction on Pacific salmon carcasses. *Ecological Entomology*, 31: 5-12.
- Hoffman, C. H., Townes, H. K., Swift, H. H., and Sailer, R. I. (1949). Field Studies on the effects of airplane applications of DDT on forest invertebrates. *Ecological Society of America*, 19(1): 1-46.
- Holloway, A. K., and Schnell, G. D. (1997). Relationship between numbers of the endangered American burying beetle *Nicrophorus americanus* Oliver (Coleoptera silphidae) and available food resources, *Biological Conservation*, 81: 145-152.
- Jurzenski, J., and Hoback, W.W. (2011). Opossums and leopard frogs consume the federally endangered American burying beetle (Coleoptera: Silphidae). *The Coleopterists Bulletin*, 65(1): 88-90.
- Jurzenski, J.D., Jorgensen, C.F., Bishop, A., Grosse, R., Reins, J., and Hoback, W.W. (2014). Identifying priority conservation areas for the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae), a habitat generalist. *Systematics and Biodiversity*, 12(2): 149-162.
- Kalinová, B., Podskalská, H., Růžicka, J., and Hoskovec, M. (2009). Irresistible bouquet of death--how are burying beetles (Coleoptera: Silphidae: Nicrophorus) attracted by carcasses. *Die Naturwissenschaften*, 96(8): 889–899.

- Kozol, A. J., Scott, M. P., and Traniello, J. F. A. (1988). The American burying beetle, *Nicrophorus americanus*: Studies on the natural history of a declining species. *Psyche: A Journal of Entomology*, 95(3-4): 167–176.
- LeConte, J.L. (1853). Synopsis of the Silphales of America, north of Mexico. *Proceedings of the Academy of Natural Sciences Philadelphia*, 6: 274-287.
- Lomolino, M. V., and Creighton, J. C. (1996). Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus americanus*. *Biological Conservation*, 77(2-3): 235–241.
- Lomolino, M. V., Creighton, J. C., Schnell, G. D., and Certain, D. L. (1995). Ecology and conservation of the endangered American burying beetle (*Nicrophorus americanus*). *Conservation Biology*, 9(3): 605–614.
- Lomolino, M. V., and Creighton, J. C. (1996). Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus americanus*. *Biological Conservation*, 77(2-3): 235-241.
- Merrick, M.J. and Smith, R.J. (2003). Temperature regulation in burying beetles (*Nicrophorus* spp.: Coleoptera: Silphidae): effects of body size, morphology and environmental temperature. *Journal of Experimental Biology*, 207: 723-733.
- Müller, J.K. and Eggert, A. (1989). Paternity assurance by "helpful" males: Adaptations to sperm competition in burying beetles. *Behavioral Ecology and Sociobiology*, 24(4): 245-249.
- Murlis, J., Elkinton, J. S., and Cardé, R. T. (1992). Odor plumes and how insects use them. *Annual Review of Entomology*, 37(1): 505-532.
- Muths, E.L. (1991). Substrate discrimination in burying beetles, *Nicrophorus orbicollis* (Coleoptera: Silphidae). *Journal of the Kansas Entomological Society* 64(4): 447-450.
- Nelson, L. Jr., and Clarke, F.W. (1973). Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy*. 56: 295-298.
- Oklahoma Mesonet. 2015. Available at <http://www.mesonet.org>. Accessed 12 November 2013.
- Santos, S.M., Carvalho, F., and Mira, A. (2011). How long do dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE*, 6(9): 1-12.
- Scott, M. P. (1998). The ecology and behavior of burying beetles. *Annual Review of Entomology*, 43(1): 595-618.
- Scott, M. P., Traniello, J. F. A., and Fetherston, I.A. (1987). Competition for prey between ants and burying beetles (*Nicrophorus* Spp): Differences between northern and southern temperate sites. *Psyche: A Journal of Entomology*, 94(3-4): 325–332.

- Scott, M. P., and Traniello, J. F. A. (1990). Behavioural and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). *Animal Behaviour*, 39(2): 274–283.
- Sikes, D. S., and Raithel, C. J. (2002). A review of hypotheses of decline of the endangered American burying beetle (Silphidae : *Nicrophorus americanus* Olivier) *Journal of Insect Conservation* 81: 103–113.
- Smith, G., Trumbo, S.T., Sikes, D.S., Scott, M.P., and Smith, R.L. (2007). Host shift by the burying beetle *Nicrophorus pustulatus*, a parasitoid of snake eggs. *Evolutionary Biology* 20 (6): 2389-2399.
- Smith R.J., Bonilla, M., Calahan, C., and Mann, J. (2000). Comparison of reproductive success of in-situ burial versus the use of abandoned burrows for carcass interment by *Nicrophorus investigator* (Coleoptera: Silphilidae). *Journal of the Kansas Entomological Society* 73: 148-154.
- Springlett, B.P. (1968). Aspects of the relationship between burying beetles, *Necrophorus* spp., and the mite, *Poecilochirus necrophori* Vitz. *Journal of Animal Ecology* 37: 417-424.
- Trumbo, S.T. (1990). Reproductive success, phenology, and biogeography of burying beetles (Silphidae: *Nicrophorus*). *The American Midland Naturalist* 124(1): 1-11.
- Trumbo, S. T., and Bloch, P. L. (2000). Habitat fragmentation and burying beetle abundance and success. *Journal of Insect Conservation* 4: 245–252.
- US Army. (2015). The Official Homepage of the US Army. Accessed 23 June 2015.
http://www.army.mil/article/138637/AMC_honors_Oklahoman_for_natural_resources_conservation/.
- (USFWS) US Fish and Wildlife Service. (1991). American burying beetle (*Nicrophorus americanus*) recovery plan. Newton Corner, MA.
- (USFWS) US Fish and Wildlife Service. (2008). ABB 5 year review: Summary and Evaluation. Newton Corner, MA.
- (USFWS) US Fish and Wildlife Service. (2014). ABB Oklahoma Presence Absence Live-Trapping Survey Guidance. Oklahoma Ecological Services Field Office, SW Region, OK.
- (USFWS) US Fish and Wildlife Service. Draft Environmental Assessment
 TransCanada's Keystone XL Pipeline LP's Gulf Coast Project (ABB range in Oklahoma). 2012.
 (a)
- (USFWS) US Fish and Wildlife Service. Species Profile: American Burying Beetle (*Nicrophorus americanus*). 27 Oct 2012. (b)
<http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?scode=I028>.
- (USFWS) US Fish and Wildlife Service. Endangered Species Program: Recovering an Illusive Gravedigger. 27 October 2012. (c)
<http://www.fws.gov/endangered/news/bulletin-spring2009/recovering-a-gravedigger.html>.

- Van Dyke, F. Conservation Biology: Foundations, Concepts, Applications. Netherlands. Springer Science & Business Media. 2008. Print.
- von Hoermann, C., Steiger, S., Müller, J.K., and Ayasse, M. (2013). Too Fresh Is Unattractive! The attraction of newly emerged *Nicrophorus vespilloides* females to odour bouquets of large cadavers at various stages of decomposition. *PLOS One* 8(3): 1-11.
- Wilson, D.S. and Fudge, J. (1984). Burying beetles: intraspecific interactions and reproductive success in the field. *Ecological Entomology* 9: 195-203.
- York, A. (1999). Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of southeastern Australia. *Journal of Insect Conservation*, 3(3), 191-199.

APPENDICES

Appendix A

	Year	Month	Low_Temp	Precip	Max_Wind	Moon	Biomass_M	Biomass_R
Year	1	-0.335516	0.083975178	0.120186	0.133871876	0.0890564	0.429614161	0.182648232
Month	-0.335516	1	-0.09184227	0.0730019	-0.282221	-0.039541	-0.144343	-0.061411
Low_Temp	0.083975178	-0.09184227	1		0.226995576	-0.117294	0.032409085	0.012968739
Precip	0.120186	0.0730019	-0.05307238	1	0.299128995	0.0648985	0.062955988	0.029265235
Max_Wind	0.133871876	-0.282221	0.226995576	0.299129	1	0.1737122	0.057506823	0.024447308
Moon	0.0890564	-0.039541	-0.11729426	0.064899	0.17371224	1	0.035952131	0.013921587
Biomass_M	0.429614161	-0.144343	0.032409085	0.02956	0.057506823	0.0359521	1	-0.11070509
Biomass_R	0.182648232	-0.061411	0.012968739	0.029265	0.024447308	0.0139216	-0.11070509	1
Sand	0.1133	-0.036768	0.032460749	-0.05721	0.015210071	0.0298575	0.545102672	0.074438933
Clay	-0.015168	0.0049222	-0.00433127	0.007615	-0.00203588	-0.004276	-0.46610783	-0.26597265
BW_M	-0.5175048	0.1737911	-0.04052754	-0.071242	-0.0692742	-0.043293	0.205122424	-0.62691521
BW_R	-0.159132	0.0536859	-0.00796441	-0.035791	-0.02129384	-0.009975	0.130219315	-0.11672801
CE_M	0.339578797	-0.113921	0.028757247	0.040069	0.04546047	0.0310212	0.889504472	-0.06835331
CE_R	0.0459984	-0.015655	-0.00020591	0.018088	0.006150756	0.0003036	-0.18800804	0.977824881
Grass	-0.00963677	0.004266	0.018122851	-0.0596	-0.00125692	0.0150038	-0.35369024	0.030229647
Forbs	0.187869723	-0.064582	-0.01261461	0.1122	0.025100723	-0.007661	-0.32917959	0.495099892
	Sand	Clay	BW_M	BW_R	CE_M	CE_R	Grass	Forbs
Year	0.1133	-0.015168	-0.5175048	-0.159132	0.339578797	0.0459984	-0.00963677	0.187869723
Month	-0.036768	0.0049222	0.1737911	0.0536859	-0.113921	-0.015655	0.004266	-0.064582
Low_Temp	0.032460749	-0.00433127	-0.04052754	-0.00796441	0.028757247	-0.00020591	0.018122851	-0.01261461
Precip	-0.05721	0.007615	-0.071242	-0.035791	0.040069	0.018088	-0.0596	0.1122
Max_Wind	0.015210071	-0.00203588	-0.0692742	-0.02129384	0.04546047	0.006150756	-0.00125692	0.025100723
Moon	0.0298575	-0.004276	-0.043293	-0.009975	0.0310212	0.0003036	0.0150038	-0.007661
Biomass_M	0.545102672	-0.46610783	0.205122424	0.130219315	0.889504472	-0.18800804	-0.35369024	-0.32917959
Biomass_R	0.074438933	-0.26597265	-0.62691521	-0.11672801	-0.06835331	0.977824881	0.030229647	0.495099892
Sand	1	-0.785039	0.027480329	0.0499	0.3977	0.0213	-0.1825	-0.4642
Clay	-0.785	1	-0.08666975	0.1426271	-0.235137	-0.251744	0.0809074	0.0554993
BW_M	0.0275	-0.08667	1	0.264414964	0.210452314	-0.54629376	-0.22550619	-0.46613267
BW_R	0.0499	0.1426271	0.264414964	1	0.313651662	-0.182061	-0.416094	-0.325626
CE_M	0.3977	-0.235137	0.210452314	0.313652	1	-0.13225982	-0.47795177	-0.31834495
CE_R	0.0213	-0.251744	-0.54629376	-0.182061	-0.13225982	1	0.091739444	0.481478047
Grass	-0.1825	0.0809074	-0.22550619	-0.416094	-0.47795177	0.0917394	1	-0.11286613
Forbs	-0.4642	0.0554993	-0.46613267	-0.325626	-0.31834495	0.481478	-0.11286613	1

APPENDIX B

Habitat characterizations for trapping grids. Values presented are averages for each grid expressed as percentages, unless otherwise noted. Measurements were taken in mid-July in 2013 and 2014, with the exception of plant biomass, which was only recorded in 2014.

Year	Habitat	Grid	BA (m ² /ha)	CC	Grass	Leaf	BG	Forbs	Rock	Woody	BM (g)	Sand	Silt	Clay	OM	TC
2013	Interior	2	9.7	23.7	7	28	13	1	26	8	--	50	27.5	22.5	3.01	SCL
		7	8.7	15.2	61	7	7	7	1	17	--	47.5	37.5	15	2.83	L
		8	7.6	12.4	22	33	4	24	0	17	--	58.8	31.3	10	1.65	SL
	Grassland	10	0	0	75	0	0	8	0	17	--	22.5	58.8	18.8	3.99	SIL
		11	0.2	0.05	66	0	0	28	0	6	--	46.3	40	13.8	2.65	L
		13	0.2	0	64	0	12	21	1	0	--	68.8	17.5	13.8	1.04	SL
2014	Interior	1	21.4	76	22	57.8	0	0	0.2	18	188	80	11.3	8.8	1.61	LS
		2	7.2	77	80	41.6	0	53	0	15.4	98	50	27.5	22.5	3.01	SCL
		3	4.8	75	84	6	0	4	0	6	543	71.3	23.8	5	1.66	SL
		7	5.8	74.3	44	43.6	0	5	0	7.4	340	47.5	37.5	15	2.83	L
		8	6.7	69.5	24	36	2	24	3	9	388	58.8	31.3	10	1.65	SL
		9	7.1	72.3	23	30	20	28	5	12	68	53.8	35	11.3	1.07	SL
	Grassland	4	0	0	57	0	8	33	0	2	398	35	40	25	1.88	L
		5	0	0	59	0	0	40	0	1	1137	62.5	30	7.5	1.36	SL
		6	0	0	82	0	0	18	0	0	--	31.3	45	23.8	3.64	L
		10	0	0	18	0	6	73	0	1	805	22.5	58.8	18.8	3.99	SIL
		11	0	0	37	0	6	48	0	9	672	46.3	40	13.8	2.65	L
		12	0	0	70	0	5	18	0	0	636	36.3	36.3	27.5	2.87	CL

* Basal area (BA), canopy cover (CC), bare ground (BG), plant biomass (BM), organic matter (OM), soil texture class (TC). Texture class is broken down into sandy loam (SL), loam (L), clay loam (CL), loamy sand (LS), sandy clay loam (SCL), silt loam (SIL).

VITA

Jessica Nicole Hoops

Candidate for the Degree of

Master of Science

Thesis: BIOTIC AND ABIOTIC FACTORS AFFECTING ABUNDANCE OF THE AMERICAN BURYING BEETLE, *NICROPHORUS AMERICANUS*

Major Field: Zoology

Biographical:

Education:

Completed the requirements for the Master of Science/Arts in your major at Oklahoma State University, Stillwater, Oklahoma in July 2017.

Completed the requirements for the Bachelor of Science in Biological Sciences at Oklahoma State University, Stillwater, Oklahoma in May 2009.

Completed the requirements for the Bachelor of Science in Animal Science at Oklahoma State University, Stillwater, Oklahoma in May 2009.

Professional Memberships:

Southwestern Association of Naturalists
National Wild Turkey Federation